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NASCENT INFLORESCENCES IN *ARCTOSTAPHYLOS PRINGLEI:* RESPONSE TO KEELEY AND WELLS

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Character states involving nascent inflorescences in *Arctostaphylos* (Ericaceae) are of great taxonomic value. Accordingly, as Keeley (1997) observes, the general absence of a nascent inflorescence in the genus is worthy of notice. *Arctostaphylos pringlei* C. Parry is a species of arid montane environments in southern California, Arizona, and northern Baja California that consists of two subspecies, subsp. *pringlei* and subsp. *drupacea* (C. Parry) P. Wells that differ in the fusion of nutlets in the fruit. The former occurs in Arizona, the latter in southern Califonrnia, and both subspecies have been found in northern Baja. Like other montane species of *Arctostaphylos,* flowering occurs between midspring through early summer. Typically, *Arctostaphylos* spp. develop a dormant (nascent) inflorescence at the tips of their new stem growth during the time fruits mature and disperse in late spring and summer. Nascents can be observed from the end of stem growth until flowering the next year. In contrast, Keeley (1997) has observed that *A. pringlei* does not produce nascents after stem growth, but produces inflorescences as flowering begins. Hence, the controversy raised by Wells (Wells, 1999) concerns the developmental timing of the formation of an inflorescence with floral buds, rather than an all or nothing type of character state, as would be implied by "nascents present versus absent."

Wells implies that Keeley's (1997) general observation is incorrect. He cites five specimens that he collected in November 1986 to demonstrate that *A. pringlei* does indeed produce nascent inflorescences. One of us (MCV) has observed *A. pringlei* in the field in northern Baja California and in Arizona. Jon Keeley had mentioned the lack of inflorescences in *A. pringlei* before a trip to the Sierra San Pedro Martir Mountains in the fall of 1995, which made it a character of interest. On November 25, 1995, one individual (and only one) was found with a nascent inflorescence; other shrubs in the area appeared to lack this structure. Given this controversy, we decided to distinguish between the separate interpretations of Keeley and Wells by posing a pair of simple alternative hypotheses: 1) the development of nascents should occur just before and during flowering (flowering phase); versus 2) the development of nascents should occur during and following fruiting (fruiting phase). Confirming hypothesis 1 and rejecting hypothesis 2 would support Keeley (1997), while confirming hypothesis 2 and rejecting 1 would support Wells (this issue).

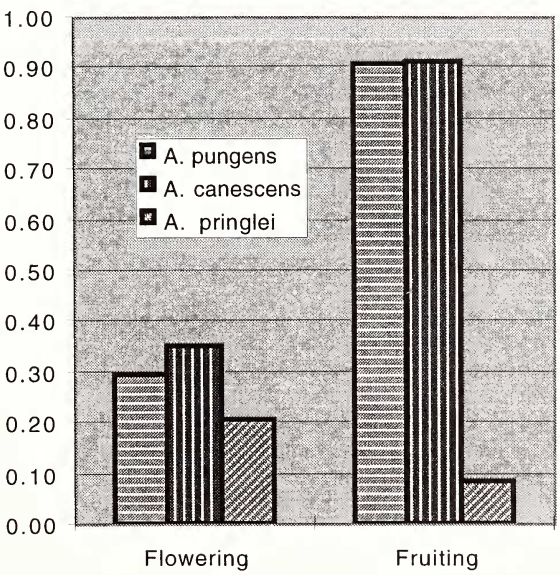
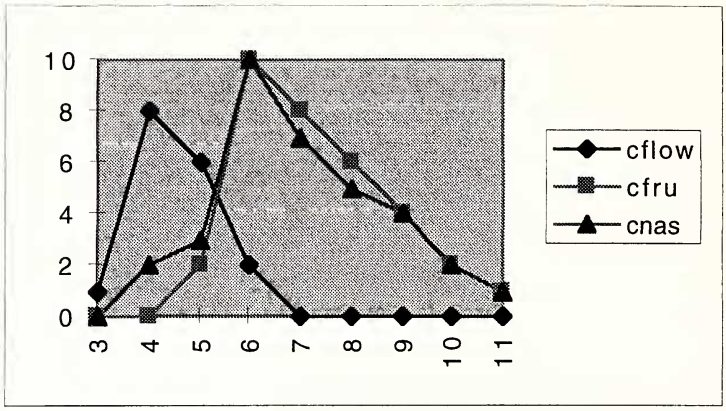


Fig. 1. Percentage of specimens examined that contained presumed nascent inflorescences for *A. pungens, A. canescens,* and *A. pringlei.* Data are presented for two phenological stages, if the specimen was in flower, and if the specimen was maturing fruit.

A



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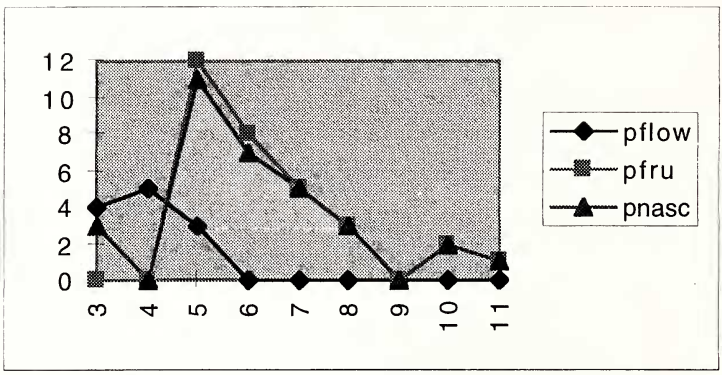

FIG. 2. Sequence of flowering, fruiting and nascent inflorescence production found in specimens housed at California Academy of Sciences. A) sequence for *A. canescens*; B) sequence for *A. pungens.*

TABLE 1. CHI-SQUARE ANALYSES OF PRESENCE OR ABSENCE OF NASCENT INFLORESCENCES AGAINST FLOWERING OR FRUITING AMONG COMBINATIONS OF *A. PRINGLEI, A. CANESCENS,* AND *A. PUNGENS.* Values in the right column include both Chi-square values and significance levels.

	Nascents	Flowering	Fruiting	Total	Chi-Square
A. pringlei	with	11	4	15	
	without	42	44	86	2.169 NS
A. pungens	with	5	29	34	
	without	12	3	15	22.572 p<<0.001
A. canescens	with	6	30	36	
	without	11	3	14	20.083 p<<0.001
A. pungens+	with	11	59	70	
A. canescens	without	23	6	29	39.653 p <<0.001
	Species	W/nascents	W/o nascents		Chi-Square
Flowering	*A. pringlei*	11	42	53	
	A. pungens+	11	23	34	2.152
	A. canescens	22	65	87	NS
Fruiting	*A. pringlei*	4	44	48	
	A. pungens+	59	6	65	79.438
	A. canescens	63	50	113	p<<0.001

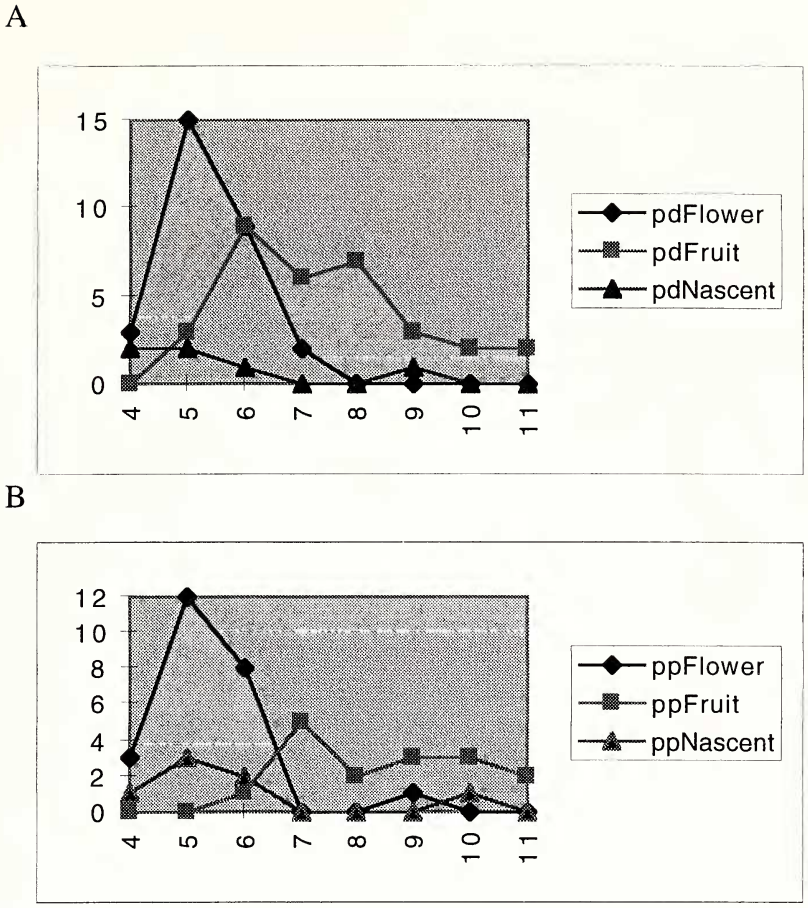

FIG. 3. Sequence of flowering, fruiting and nascent inflorescence production found in specimens housed at California Academy of Sciences. A) sequence for *A. pringlei* subsp. *drupacea*; B) sequence for *A. pringlei* subsp. *pringlei.*

METHODS

Initially, 101 sheets of specimens from the California Academy of Sciences (CAS) of both subspecies of *A. pringlei* collected throughout its range were examined for phenological stage and presence or absence of apparent nascent inflorescences (note: shortly prior to flowering, immature inflorescences appear similar to "nascents"). Collection numbers for each sheet were recorded as well as dates of collection, county, phenological stage (early flowering, flowering, early fruiting, fruiting, and past fruiting), and presence or absence of nascent inflorescences. For comparative purposes, two other mid-montane species, 49 sheets of *A. pungens* and 50 sheets of *A. canescens,* were examined in a similar way (a total of 99 sheets for the two species combined). Chi-square 2 × 2 contingency analysis was used to test for differences in nascents between flowering and fruiting stages (Zar 1984).

RESULTS

Arctostaphylos pungens Kunth and *A. canescens* Eastw. are typical of other species in the genus. The development of nascent inflorescences occurs at the time fruits are maturing on the tips of newly elongating stems (Fig. 1, 2). Approximately 90% of the specimens in the fruiting phase are developing nascent inflorescences. Note that this pattern holds true for both of these species and there is no significant difference between them (Table 1). *Arctostaphylos pringlei* is not substantially different from the other two species during the flowering phase (Fig. 1, 3), however, during the fruiting phase, less than 10% of the *A. pringlei* specimens possessed nascent inflorescence structures (Fig. 1, 3). This pattern held true equally for both subspecies suggesting that this unusual developmental character is a shared feature in the *A. pringlei* lineage. The stark contrast between *A. pringlei* and the other species during the fruiting phase (Fig. 1, Table 1) are consistent with our hypothesis 1, which supports the conclusions of Keeley (1997).

Granted, four out of 48 specimens of *A. pringlei* were found to present nascent inflorescences apparently established during the fruiting phase. We underscore "apparently" given the possibility that these individuals represent shrubs that may be flow-

ering out of season. One CAS specimen (#563576), for example, was flowering in September, clearly an "exception from the rule" that may be associated with phenological opportunism on the part of this individual; such opportunism is common in the genus. In contrast, 59 out of 65 sheets of *A. pungens* and *A. canescens* had nascents during the fruiting phase (Fig. 1, 2). This difference in the pattern of nascent inflorescence establishment between *A. pringlei* and other species of *Arctostaphylos* during the fruiting phase is significant. These findings are very consistent with the observations of Keeley (1997).

Discussion

Given its near universal occurrence in *Arctostaphylos,* the nascent inflorescence developmental character is logically ancestral in this genus. In that case, the general lack of nascent inflorescences in *A. pringlei* during the fruiting phase is likely a derived condition. With this feature combined with its unusual pink deciduous bract characters, characters that Wells (1992) interpreted as warranting subsectional status for this species, *A. pringlei* appears to be a distinctive lineage within the genus. Keeley (1997) introduces an important observation concerning the general lack of nascent inflorescences in *A. pringlei.* Our analysis of specimens from CAS confirms his observations with nascents rarely occuring during the fruiting phase in *A. pringlei* in decided contrast to other species in the genus in which a large majority of individuals establish nascents during this phenological stage (Fig. 1, 2, 3, Table 1).

Having observed numerous populations of *Arctostaphylos* in the field, we have come to the conclusion that few single characters are completely consistent in this genus. Instead, within *Arctostaphylos,* consistency is revealed in a suite of characters that distinguish species reliably. That rare exceptions occur to the "lack of nascent inflorescence" status of *A. pringlei* is hardly surprising. Taking the position that "exceptions must make the rule" in this instance and that Keeley's two years of population observations are somehow uninformed or incorrect seems unlikely to advance our understanding of this complex group.

Literature Cited

Keeley, J. E. 1997. Absence of nascent inflorescences in *Arctostaphylos pringlei.* Madroño 44:109–111.

Wells, P. V. 1999. Nascent inflorescences in *Arctostaphylos pringlei.* Madroño. 46:49–50.

Zar, J. H. 1984. Biostatistical analysis, 2nd ed. Prentice-Hall, Inc., Englewood Cliffs, NJ.